

The association between the mealybug, *Pseudococcus macrozamia*, ants and the cycad *Macrozamia reidleyi* in a fire-prone environment

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Abstract

The mealybug, *Pseudococcus macrozamia*, was found on the cycad, *Macrozamia reidleyi*, near Jandakot, Western Australia. In 1979, *M. reidleyi* plants which had not been burnt for at least 10 years had fewer leaves, fewer distortions to leaflets and less mealybugs when compared with plants that had regenerated from burns in 1977 and 1978. Where present, the mealybugs were found at the base of leaves or where leaflets were forced together or were distorted by fire. Ants were found with all colonies of mealybugs. The exclusion of ants did not affect the abundance of mealybugs, nor were ants necessary for the establishment of mealybug colonies. We suggest that ants are incidental in this mealybug/plant association and both the mealybug and the plant respond favourably to increased fire frequency.

Introduction

Fire is an important feature of Australian ecosystems. Many plants show adaptations to survive fire, some even require fire for reproduction, seed release, germination and new growth (Gill 1975). These fire-induced changes in plants are likely to affect obligatory plant feeders such as homopterans. After a fire insects may respond either by initial population decrease that slowly returns to the pre-fire level, as do certain stick insects (Campbell 1961), or by an immediate response to the presence of new growth on the plant, resulting in a large population after the fire. This then decreases to the pre-fire level as with the mealybugs in this study. Few other examples of the latter response are known (Gillon 1971) and there are no documented cases involving homopterans, although such a response by this taxon has been suggested by Tippins (1972).

Some homopterans extrude excess sugars as honeydew while feeding on plants. Ants are attracted to the honeydew, and incidentally provide benefit for the homopterans. Such mutualistic associations are well documented for agricultural ecosystems (Nixon 1951, Way 1963) but not for natural systems (Miller and Kosztarab 1979). Studies in agricultural situations show these associations to vary from obligatory to incidental. The homopterans may benefit in the following ways: the removal of honeydew and therefore reduction of sooty-mould infestations; the removal of dead individuals; protection from predators and parasites; transport to overwintering sites, and the colonization of new areas (Nixon 1951, Way 1963). In exchange, the ants are provided with a reliable source of live and dead individuals, as well as a supply of honeydew. The predation by ants is usually at a low level, not threatening the survival of the homopteran population (Way 1963).

An association between ants and the mealybug, *Pseudococcus macrozamia* (Fuller) (Homoptera: Pseudococcidae), occurs on the cycad, *Macrozamia reidleyi* (Gaud.) C. A. Gardn., in an area of natural bushland near Perth, Western Australia. Some parts of this area are subject to frequent fires. We initiated a study, directed towards three specific questions associated with the interaction between mealybugs, plants and ants. Firstly, what role does fire play in the occurrence of mealybugs on *M. reidleyi*? Secondly, does the abundance of mealybugs differ in the presence or absence of ants? Thirdly, are ants necessary for establishing new mealybug colonies?

Species biology

Macrozamia reidleyi is found in the south-western part of Western Australia. It is a small shrub with a mainly subterranean bulb with leaves standing up to 2 m. It forms a conspicuous part of the understorey of the *Banksia* woodland in the area studied at the Marsupial Breeding Station near Jandakot (32°10'S; 115°50'E). Vigorous growth of new leaves occurs after a fire and 1-2 years later there is an increase in the production of reproductive structures (Baird 1977).

The mealybug, *Pseudococcus macrozamia*, was specific to *M. reidleyi* at the study site. It favoured protected sites on the plants, the most abundant being at the bases of the leaves where there was protection by the cotton-like growth on the bulb, and on new growth where the leaflets were held together to form a partially closed environment. Enclosed habitats located distally on leaves may be formed by immature leaves which have been damaged by fire. Damaged leaflets remain on the leaves after the latter emerge from the bulb, and in this paper are

referred to as 'crinkled' habitats. Other habitats of closely associated leaflets occurred most commonly on new leaves and where damaged leaflets were held together by resin-like substances from wounds on the leaf. These, as well as leaflets held together by stems of climbing plants, are referred to as 'straight' habitats.

Fire removed exposed leaves from the cycad, leaving the bulb and bases of the leaves. Insects on these exposed leaves were burnt, whereas those within the cotton like substance at the base of the leaves could survive. This is shown by the presence of adult mealybugs soon after a fire.

The mealybugs appeared to reproduce throughout the year because young were present at all times. We found no alates and presumed that reproduction was entirely parthenogenetic. There were four instars and an imago (J. Dolva, unpublished observation).

Two species of ant, *Iridomyrmex chasei* Forel and *Camponotus* sp., were found with the colonies. The mealybugs feeding between the leaflets were not always accessible to these ants, however, mealybugs may move to the edge of leaflets where they are tended.

A number of other insects was found with the mealybug colonies including: Blattodea species nymphs; one Chrysopidae larva which was covered in wax resembling that of the mealybugs; *Cryptolaemus montrouzieri* (Coccinellidae) adults and larvae; Araneida and Pseudoscorpionidae, some of which may be predators on the mealybugs. The beetle, *C. montrouzieri*, is known to eat scale insects at the study site and Chrysopidae larvae are known to eat homopterans. The araneida probably eat ants (B. Main, pers. comm.). None of these arthropods were present in large numbers. *C. montrouzieri*, which was the most abundant predator, was found on 22.6% of mealybug colonies in a survey of 31 colonies on 65 plants.

Methods

Effect of fire

We surveyed plants during March 1979 in areas burnt in March 1977, November 1978 and a third area not burnt for at least 10 years. We counted the number of leaves in all areas and measured the length of leaves in the 1978 burn area and the pre-1969 area. We noted the presence of crinkled leaflets and mealybugs in each area.

Ant exclusion experiment

In the 1977 burn area, we selected 12 plants with mealybug present in 'crinkled' habitats on the distal parts of leaves. Below the colonies we placed 'tanglefoot' (Tanglefoot Company, Grand Rapids, Michigan) to prevent invasion by ants and to stop migration of mealybugs to base of the leaves. All leaflets and other material which may have provided a bridge for the ants to the isolated colony and any ants remaining on the colony were removed by hand. Ten similar sized colonies were selected as controls. These were marked for later identification but were otherwise unchanged. After 115 days the leaves of the mealybug habitats were prised apart and the insects counted. The duration of the experiment allowed for at least 2 generations of mealybugs to develop. We counted the mealybugs in 3 size classes (first and second instar, 2 mm;

third and fourth instar, 2-4 mm; imago, 4 mm). Insects were not counted at the start of experiments because this method destroys the habitat.

Because the initial number of insects was not known, differences in population sizes were analysed by controlling for the size of the colony. Analysis of covariance (Li 1964) was used with the number of sides of leaflets occupied by the mealybugs ($\log(x + 1)$ transformed) as the independent variable. The dependent variables were counts of the 3 size classes and total number of mealybugs ($\log(y + 1)$ transformed) and the regression lines were compared between samples with and without ants.

Importance of ants for colonization

To test whether the presence of ants was necessary for the successful establishment of new colonies, we made 19 artificial colonies in the recently burnt areas. These were made by binding together 4 leaflets with waterproof adhesive tape. This produced habitats similar to a number of naturally occurring straight habitats, where leaflets had been forced together. Artificial habitats were arranged, 3 per leaf, on the top, middle and bottom. Four adult mealybugs were introduced into each habitat. Ants were excluded from some of the leaves ($N = 7$) by the use of 'tanglefoot'. After 115 days we collected the colonies and counted the mealybugs.

Results

Effect of fire

Plants from the area which had not been burnt recently had over a third fewer leaves than plants in recently burnt areas (Table 1). The length of leaves was similar between areas. The presence of crinkling of leaflets was associated with burnt areas (Table 2). Crinkling did not occur at all in our sample from the area which had not been burnt

Table 1

Mean \pm standard error of length and number of leaves of *M. reidley* for areas with different fire histories. ANOVA on number of leaves, significant at $p < 0.001$. T-test on length of leaves, not significant.

Year burnt	No. of leaves per plant (N = No. of plants)	Length of leaves (cm) (N = No. of leaves)
pre 1969	8.0 \pm 1.45 N = 21	125.1 \pm 3.74 N = 153
1977 ..	13.5 \pm 0.77 N = 54	No data
1978	13.0 \pm 1.01 N = 48	130.7 \pm 0.04 N = 479

Table 2

Occurrence of crinkled habitats in areas of different fire histories. Fisher exact probability test, significant at 0.001 level

	Crinkled leaflets on plants	
	Present	Absent
Burnt before 1969	0	21
Burnt in 1977 or 1978	15	97

recently whereas in the burnt areas about 15% of plants exhibited this type of damage. All crinkled habitats investigated were occupied by mealybugs in the 1977 burn area. Mealybugs were starting to occupy crinkled habitats in the 1978 burn area during our study. There were from one to 57 gaps between leaflets on each leaf for the mealybug to occupy (mean \pm S.E., 14.3 ± 0.12 , $N = 128$ crinkled habitats).

Mealybugs were more common on plants in the areas that had been recently burnt (Table 3). Less than 10% of plants in the area burnt before 1969 had mealybugs, compared with about 20% for the 1977 burn. The 2 colonies of mealybug were at the bases of 2 plants in the area burnt before 1969. In the 1977 burn area all plants with mealybugs had basal colonies; 60% had distal straight colonies and 40% had distal crinkled colonies.

Ant exclusion experiment

Ants were always found with colonies of mealybug. Larger mealybug colonies, as measured by the number of gaps that were occupied, had more ants

present ($r = 0.943$, log/log transformation, 24 d.f. $p > 0.001$). Different species of ant were associated with different types of mealybug colonies (Table 4). More (36%) of *I. chasei* individuals occurred distal on leaves than *Camponotus* sp. (19%).

Except for the control treatment for the large instars and the imagines, a relationship was found between the abundance of the mealybugs and the number of sides of leaflets showing signs of mealybug occupation (Table 5). The low coefficients of determination for both these controls were partially due to one large colony which was found to have few large instars and no imagines. However, even with these values included, there was an overall significant regression equation for the analysis of covariance (Table 5). The slopes of the lines and the mean number of mealybugs calculated from the overall mean size of colony did not differ between the controls which had ants in attendance and the experimental colonies where the ants had been removed (F tests). Similarly, in both the experimental and control groups, the ratio of young per adult did not differ (t-test, $t = 1.34$, 16 d.f. N.S.).

Importance of ants for colonization

Colonies of mealybug became established in all artificial habitats. After 115 days there were over twice as many individuals of all instars and imagines at the habitats on the bottom on the leaves (Table 6).

When ants were excluded from artificial colonies, the total number of insects did not differ from artificial colonies with ants (Table 7). Apart from the result for the number of imagines, it seemed that colonization did not require ants. It was likely that the difference in the number of imagines was due to mortality or migration as the abundance of instars was similar between treatments.

Discussion

Fire, which was necessary for healthy growth and reproduction of *Macrozamia reidleyi* (Baird 1977) also benefited *Pseudococcus macrozamia*. We found that with long absence of fire plants produced few leaves. In unburnt areas there were fewer plants with mealybugs. Possible reasons for this are decreased health of plants, absence of suitable habitats and increased predation. Following a fire mealybugs which had survived at the base of leaves colonized new growth and in due course distal habitats.

Table 3

Occurrence of mealybugs on plants with different fire histories. Fisher exact probability test significant at 0.005 level

	Number of plants	
	Mealybugs present on plants	Mealybugs absent on plants
Burnt before 1969	2	19
Burnt in 1977	33	79

Table 4

Comparison of the habitat choice of individual ants tending colonies of mealybugs. $\chi^2 = 8.89$, 1 d.f., $p < 0.001$

Location of ants on tended colony	Number of ants	
	<i>I. chasei</i>	<i>Camponotus</i> sp.
At base or on new fronds	55	140
Distal on fronds	31	33

Table 5

Regression of the numbers of small instars, large instars and imago and total mealybugs ($\log(y + 1)$ transformed) (Y 's) with the numbers of sides of leaflets showing signs of occupation ($\log(x + 1)$ transformed) (X 's) with and without ants

Dependent variable	Treatment (ants)	N	Regression equation	r^2	Probability $\beta = 0.0$	Adjusted number of mealybugs*
Small instars	present	10	$Y = -2.74 + 1.94X$	0.71	< 0.05	47.4
	excluded	12	$Y = -1.63 + 1.45X$	0.79	< 0.01	26.7
Large instars	present	10	$Y = 0.86 + 0.41X$	0.39	$0.2 < p < 0.1$	8.7
	excluded	12	$Y = -0.20 + 0.75X$	0.72	< 0.01	9.8
Imago	present	10	$Y = 0.49 + 0.34X$	0.26	$0.5 < p < 0.4$	4.2
	excluded	12	$Y = -0.45 + 0.67X$	0.73	< 0.01	5.2
Total mealybugs	present	10	$Y = -0.97 + 1.52X$	0.66	< 0.05	68.4
	excluded	12	$Y = -0.98 + 1.42X$	0.85	< 0.001	47.9

*Adjusted to $X = 3.42$ (i.e. 29.6 sides of leaflets) which represents the average sized colony.

Table 6

Mean \pm standard error of numbers of mealybugs in artificial colonies with ants on three sites along the leaves on 12 *M. reidleyi* plants. Kruskal-Wallis one-way ANOVA was significant at 0.05 level for imago and large instars and significant at 0.01 level for the small instars and total mealybugs

	Position on frond		
	Top	Middle	Bottom
Small instars	22.4 \pm 10.98	50.4 \pm 20.75	133.3 \pm 25.89
Large instars	6.3 \pm 1.74	5.9 \pm 1.96	12.8 \pm 3.35
Imago	1.5 \pm 0.47	3.4 \pm 1.20	8.3 \pm 3.11
Total mealybugs	29.3 \pm 10.83	59.8 \pm 22.66	155.7 \pm 28.43

Although ants were always found with mealybug colonies, the association was not obligatory for mealybugs. Survival, reproduction and the establishment of new colonies of mealybugs was not dependent on the presence of ants. The mealybug is mobile, lives in protected habitats, is host specific and tended by more than one species of ant. Other species of *Pseudococcus* with similar biology have analogous relationships with ants (Strickland 1950, Way 1963) but contrasting obligatory relationships have been described for many Homoptera (Das 1969, Way 1954). These latter Homoptera are sedentary, often exposed, host generalists and they are frequently tended by only one species of ant.

The mealybugs were more abundant lower on leaves and most abundant at the bases. We saw exposed adults moving on leaves and we suggest this is the means by which colonization occurs within plants. We do not know how the mealybugs arrive at new host plants. Strickland (1950) and Way (1963) give examples of *Pseudococcus* being carried to new habitats by ants. This possibly does not occur with *P. macrozamia* as ants were never seen carrying the mealybugs. Some bushes were touching and it is likely that such closely adjacent bushes are directly colonised by moving adults or instars. Colonization by wind is another possibility since exposed individuals can be dislodged (McClure 1979).

It is still not clear what combined role ants, predators and fire play in the maintenance of the mealybug population. It is apparent that fire, which stimulates new plant growth and provides new mealybug habitats, is important to this homopteran-host plant relationship, and ants are of minor importance to the survival, reproduction and colonization of this mealybug.

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Table 7

Mean \pm standard error of numbers of small instars, large instars, and imago mealybugs from artificial colonies with and without ants on plants burnt in 1977. Mann-Whitney U Test was significant at 0.01 level for imago but was not significant for instars and total mealybugs

	Sample size (colonies)	Small instars	Large instars	Imago	Total mealybugs
Ants present	12	54.7 \pm 26.31	6.8 \pm 2.07	3.2 \pm 1.06	64.7 \pm 23.74
Ants absent	7	46.1 \pm 16.66	10.0 \pm 2.97	12.6 \pm 4.82	62.3 \pm 28.34

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